

THE BIOLOGY OF *TRICHOPODA PENNIPES* FAB.
(DIPTERA, TACHINIDÆ),

A PARASITE OF THE COMMON SQUASH BUG.*

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PART I.

INTRODUCTION.

The common squash bug, *Anasa tristis* de Geer, is an ever-present and often troublesome pest in Massachusetts, and has been a subject for investigation at the Massachusetts Agricultural Experiment Station for the past three years. While studying the life history and habits of this pest, the writer discovered abundant evidence of the presence and activity of the parasite *Trichopoda pennipes*. A review of the literature showed that comparatively little is known of the life history and habits of this beneficial fly. Much to the surprise of the writer, in view of his own observations, it was found that some authors have even intimated that little good is derived by mankind from the work of this supposedly beneficial species.

Failure of the written records to substantiate observations of the writer furnished the initial stimulus to a study of the habits of the fly, the object of this study being to discover the exact relationship existing between parasite and host. A portion of the following account is the result of these studies.

During the course of the work it was found necessary to confine adults of both sexes in the same cage to induce mating. Some difficulty was experienced at first in determining the sex

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of living flies, without undue handling, and this led to a study of the external anatomy of the species, the primary aim being the discovery of secondary sexual characters that might be readily recognized.

The scope of this investigation has gradually increased, and in this paper takes the form of an exposition of the external morphological characters of the species. These characters are here designated according to the most widely accepted view of leading workers in insect morphology, and thereby do violence to the terminology in common use among taxonomic workers. This is perhaps unfortunate, but it is unavoidable, if morphological accuracy is to be maintained.

SYNONYMY.

The species was first described by Fabricius (1794)¹ as *Musca pennipes*, from material secured from the "Carolinas." His subsequently described *Thereva hirtipes* (1805, p. 219.9), *Thereva pennipes* (1805, p. 219.8), and *Ocyptera ciliata* (1805, p. 315.9) have proved to be synonyms. His *Dictya pennipes* (1805, p. 327.5) is a change of genus from *Musca*. Other synonyms are *Phasia jugatoria* Say (1829), and *Trichopoda flavicornis* and *T. haitensis* of Robineau-Desvoidy (1830). The genus *Trichopoda* was erected by Latreille (1829), and both Wiedemann (1830) and Robineau-Desvoidy (1830) soon placed the *Musca pennipes* of Fabricius in this genus. The *T. pyrrhogaster* and *T. ciliata* of Wiedemann (1830) have since fallen as synonyms, Brauer and Bergenstamm (1891) showing that these were but females of the species. The complete synonymy, so far as can be determined by the writer, is included in the bibliography at the end of this paper.

GEOGRAPHICAL DISTRIBUTION

The genus *Trichopoda* belongs to the New World fauna. *T. pennipes* has a wide distribution in both North and South America and among the adjacent islands, according to Townsend

¹Dates in parenthesis refer to the bibliography.

(1893), who records it from Argentina, Brazil, Mexico, San Domingo and Jamaica, and in the United States from New England to Florida, along the coast of the Gulf of Mexico to Texas, and in California. He speaks of it also from Michigan, Illinois, Indiana, and Iowa. It is essentially a lowland form, being most abundant within its range at elevations of five hundred feet or less. Aldrich (1915) states that the species "appears to occur from Argentina north to about the latitude of Kansas, and further north to the eastward, but not in the northwest." Records of its capture in St. Vincent, Porto Rico, and other islands of the West Indies are given in Aldrich's Catalogue (1905). Wilson (1923) adds St. Croix, of the Virgin Islands group, to this list.

HOSTS.

The first record of the life history of *Trichopoda pennipes* appears to be a note by Packard (1875) of a Tachina fly parasitic upon the squash bug (*Anasa tristis* de Geer, Hemiptera, Coreidæ.) While the species is not mentioned, the description points quite conclusively to *T. pennipes*. A. J. Cook (1889) records the insect by name and gives an account of its habit of parasitizing the squash bug. Later authors recording it as a parasite of the squash bug were Coquillett (1897), Chittenden (1899), and Weed and Conradi (1902). For a number of years no other host was known, but Morrill (1910) recorded a rearing of *T. pennipes* from the Northern Leaf-footed Plant Bug (*Leptoglossus oppositus*, Hemiptera, Coreidæ). Jones (1918) records it as an enemy of the Southern Green Plant Bug or Pumpkin Bug (*Nezara viridula*, Hemiptera, Pentatomidæ), and Watson (1918) also records this host in Florida, Drake (1920) also reared this parasitic fly in Florida from the Green Soldier Bug (*Acrosternum hilaris*, Hemiptera, Pentatomidæ), the Green Stink-bug (*Acrosternum pennsylvanicum*) and a large Coreid, *Archimerus calcarator*. He also noted eggs on *Acanthocephala femorata* and *A. declivis*. Wilson (1923), in collecting *Nezara viridula* on the Island of St. Croix, found 93 per cent of the specimens parasitized by *T. pennipes*.

Mr. H. J. Reinhard, entomologist of the Texas Agricultural Experiment Station and a specialist in Tachinidæ, says in correspondence with the writer that in Texas *T. pennipes* is parasitic upon *Nezara viridula* and *Leptoglossus phyllopus*. He adds, "I have observed adults depositing eggs on the adult Harlequin Bug (*Murgantia histrionica*, Hemiptera, Pentatomidæ) but have never been able to obtain any emergence of the parasite."

In Massachusetts this beneficial insect is important as an enemy of the squash bug, and in the following pages it is treated in its relation to this host.

Methods employed.

The following account of the life history and habits of *Trichopoda pennipes* has been taken from field and laboratory records compiled by the writer during an investigation of the squash bug. Collections of the bugs in the field furnished parasitized material for breeding purposes and also indicated the percentage of infestation. In the laboratory the parasitized bugs were kept in breeding cages containing small potted squash plants. The cages used were devised at this Station, and are so built as to afford a maximum of light. A vertically-sliding pane of glass comprises the door, and this, together with a hinged glass top, allows all corners of the cage to be readily observed from the outside. The sides and back of the cage may be covered with fine-mesh cloth screening, or with copper wire cloth. During this investigation, the cages rested on pieces of slate covered with an inch of soil, to provide normal conditions for pupation of the parasite.

LIFE HISTORY.

The Egg. The female fly lays its eggs upon the body wall of the host, to which the eggs are firmly attached. The great majority of the eggs are found on the sides of the abdomen and thorax, although they are sometimes seen fastened to the upper surface of the body and the head, and rarely to the antennæ and legs.

The length of time necessary for the hatching of the egg was found to be in the neighborhood of thirty hours. To prove

this point eggs were removed from the body of a bug as soon as laid, a moistened camel's hair brush proving to be excellent for this purpose, and were isolated in vials. After twenty-four hours the mouth-hooks of each young maggot could be seen rasping away at the inner surface of the egg-shell, and in thirty hours the larva was found protruding from the hole it had scraped in the floor of its prison. Eggs removed from the body surfaces of bugs thirty hours after oviposition were found to be empty, a hole in the bottom of each, and a corresponding hole in the chitin of the host, testifying to the penetration of the parasite.

The Larva. As stated above, the larva, upon hatching, penetrates the bottom of the egg-shell and burrows directly through the body-wall of the host, regardless of the thickness of chitin at that particular point.

Sufficient dissections of parasitized squash bugs have not been made to enable the writer to state accurately the habits of the parasite within its host, or the number of larval instars. Individuals of three different instars have been observed, and it is probable that there are four in all, as has been stated by Townsend (1908, p. 98) for certain other Tachinid parasites. Dissections seem to show that the larvæ while young live in the general body-cavity, no derangement of organs being apparent in these dissections. As the larvæ approach maturity, however, they gradually consume the fat body and those organs contained in the abdomen of the host, which was seen to be practically hollow in some adult squash bugs from which parasites had just emerged.

Upon the completion of growth, which requires approximately sixteen days, the larva forces its way out at the posterior end of the body of the host, which is still alive, and drops to the ground. This is not the case with the second generation larvæ, which appear to remain within the body of the host throughout the winter, completing their growth when the latter become active in the spring. The host dies within a day or two of the emergence of the parasite. Emergence through the side of the body, as recorded by Weed and Conradi (1902), has not been observed.

The Puparium. Within a few hours of the time the mature larva quits the host, it burrows into the soil to a depth of one to two inches, and there pupates within the last larval skin, which forms the puparium. The pupa, then, falls in the first class as defined by Thompson (1910, p. 284), and probably has a rapid early development. Dissections of the puparia have not been made, and thus the appearance of the pupa and its rate of development are unknown. The pupal period of the spring generation is approximately a month in length, while that of the summer generation lasts from thirteen to nineteen days.

The Adult. The flies are able to take wing within a few seconds following emergence, and have been observed to mate within twenty-four hours. The length of time which then ensues before oviposition commences is not known, nor has the average number of eggs laid per female been determined. One fly laid thirty-nine eggs in twenty-four hours, and another, when captured in the field, contained over one hundred eggs.

In the cages, honey-water on sponges failed to attract the flies. They were captured in the field from the flowers of Wild Carrot (*Daucus carota*) and Meadow Sweet (*Spiraea salicifolia*) and would feed from these flowers in the cages. The writer did not learn of Townsend's (1908, p. 110) method of feeding, using dry sugar and sponges moistened with water, until too late to use it in the breeding work.

The behavior of caged females toward the bugs confined with them was interesting to observe. The urge to lay eggs did not appear to be constant. At times the flies would walk about among the bugs, with apparent friendliness, and would even crawl over them without making a menacing movement. At other times a fly would dart at a bug and alight upon its back, and the writer would focus his attention in the expectation that an egg would be laid. The fly would turn this way and that upon the unresponsive host, as if trying to decide where to place the egg, but after a few seconds would walk off, as if having changed its mind, leaving no egg behind. When oviposition actually took place, the act was accomplished with great rapidity, the fly seeming scarcely to come to rest upon its host. That no such speed was necessary could be seen in the lack of

interest displayed by the victim, which neither resisted the attack of the fly nor tried to dislodge the egg.

RELATION BETWEEN PARASITE AND HOST.

Various observers have noted the parasitic habit of *Trichopoda pennipes* and have speculated upon the amount of benefit derived from its activities. Thus Dr. A. S. Packard (1875) says, "The larvæ are very large, one specimen only occurring in the body of the *Coreus*, which seems apparently healthy, and performs its sexual functions in spite of the presence of so large a parasite." Chittenden (1899) observes that "Although these flies appeared soon after the advent of the bugs and in considerable abundance, they seemed to accomplish little in the direction of reducing the numbers of their host.—The parasitized individuals were not noticed to die much earlier than those which succumbed to natural causes." Weed and Conradi (1902)

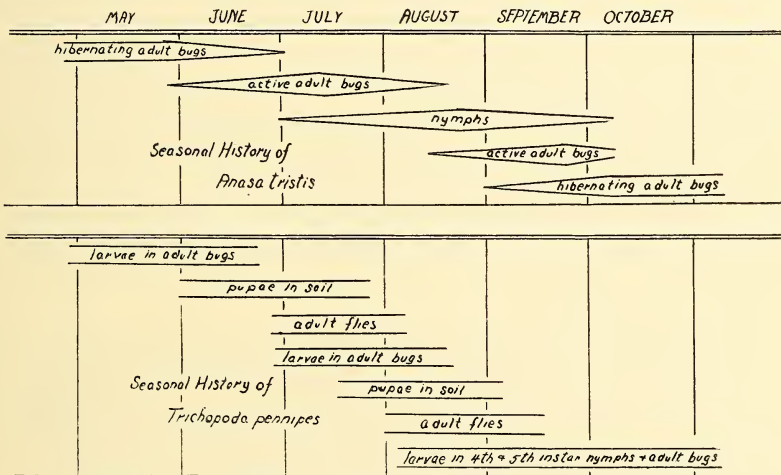


Fig. 1. Relation of *Trichopoda pennipes* to its host, *Anasa tristis*, Amherst, Massachusetts, 1922. Worthley (1923).

also mention the continued egg-laying of parasitized squash bugs. Drake (1920) in his notes on *T. pennipes* as a parasite of the Southern Green Stink-bug mentions percentages of parasitism ranging from 31 to 80 per cent.

About Amherst, Massachusetts, *Trichopoda pennipes* appears to have two full generations each year (Worthley, 1923). A single adult captured in October may indicate a partial third generation, but it is thought more probable that this was a laggard individual of the second generation.

The emergence and pupation of second generation larvæ in the fall was not observed in the cages, and it therefore appears that the parasite passes the winter as a larva within the body of the hibernating host. Development of these larvæ is completed in the spring, emergence from the host and pupation occurring during June and July. This emergence is shortly followed by the death of the host, which, in all cases so far observed, has not been able to commence egg-laying.

Pupæ developing from these overwintered larvæ begin to yield flies in late June. At this time only adult squash bugs are available, and upon these the flies deposit their eggs. These bugs are individuals which escaped parasitism the previous fall, and have lived to mate and lay eggs. Many of them are actively engaged in oviposition when attacked by the parasite, and these can often complete their egg-laying before the activities of the maggots become fatal. One female squash bug laid a cluster of viable eggs just six days previous to her death from parasitism, showing that the metabolism of the host is not seriously unbalanced until late in the development of the parasite. It is this apparent slight effect of parasitism on the egg-laying bugs which has caused investigators to question the efficiency of the parasitism of *T. pennipes*.

While parasitized egg-laying squash bugs may be permitted to complete a practically normal existence, as has been shown above, the parasite itself may not be so well favored. Thus adult bugs begin to disappear from the fields about the middle of July, having completed the normal span of life. Parasite flies are actively laying eggs at this time, and often deposit them upon bugs which are destined to die before the parasitic larvæ have attained full growth. In such cases the parasite cannot complete its development, and perishes with its host.

Larvæ which have been more fortunately situated mature and pass on to the pupa stage during the latter part of July and

early August. When these pupæ yield adult flies during August and the first part of September, many young squash bugs have become adult, and more have reached the fourth and fifth instars. Upon these bugs the parasite lays its eggs, and it is in this generation that the work of the fly is seen to be effective beyond question, since no parasitized bug appears to live to sexual maturity. Many nymphs (counts have shown about 50 per cent) die before becoming adult, and those which reach the adult state and pass the winter safely in hibernation, are subsequently killed by the parasite before laying eggs.

No parasites appear to reach maturity in nymphs which die. In this regard the egg-laying flies seem unable to discriminate closely between nymphs which are sufficiently developed to support the parasite maggots and those which contain too little substance. However, the flies seem to realize that their progeny will find too little nourishment in nymphs younger than the fourth instar, since third instar nymphs were rarely molested in the cages, and parasitized third instar nymphs were not collected in the field.

It was interesting to note that occasionally a nymph would escape parasitism by molting, leaving an unhatched parasite egg on the molted skin. This does not account for any great loss, however, since the egg of the parasite hatches in thirty hours, while the fourth and fifth instars of the squash bug require about six days and sixteen days respectively for their completion.

But one parasite has ever been observed to issue from one host. Several maggots have been observed to enter one host, but this has always seemed to result in the early death of the host and of the parasites within.

Collections of squash bugs in the fall give no indication of the true percentage of parasitism, since many nymphs die, and others slough off the empty egg-shells of the parasite with their molted nymphal skins. In midsummer, however, collections of overwintered adult bugs have indicated a parasitism as high as 80 per cent. There is no reason to suppose that the percentage of parasitism may not often run as high among the older nymphs

and new adult squash bugs in the fall. Thus it would seem that the activities of *Trichopoda pennipes* furnish an exceedingly important natural check upon the increase of *Anasa tristis*.

SUMMARY

Trichopoda pennipes is a parasitic fly belonging to the family Tachinidæ. The species enjoys a wide distribution in the lowlands of North and South America and the adjacent islands, and has been recorded as attacking several species of insects belonging to the hemipterous families Coreidæ and Pentatomidæ. Among these hosts is the common squash bug, which in Massachusetts is the principal host, and possibly the only one attacked by the fly.

The investigations recorded in this paper indicate that in Massachusetts this parasite passes through two full generations annually. Adults of the first generation deposit their eggs on egg-laying adult squash bugs, during July. Those of the second generation attack the older nymphs and new adult bugs in August and September. Collections of squash bugs have indicated a parasitism of eighty per cent. Squash bugs which are parasitized in the fall apparently do not live to sexual maturity, and thus an important natural check is placed upon the increase of the squash bug.